Lethal Aggression in Pan Is Better Explained by Adaptive Strategies Than Human Impacts

Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts

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Observations of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) provide valuable comparative data for understanding the significance of conspecific killing. Two kinds of hypothesis have been proposed. Lethal violence is sometimes concluded to be the result of adaptive strategies, such that killers ultimately gain fitness benefits by increasing their access to resources such as food or mates.[1-5] Alternatively, it could be a non-adaptive result of human impacts, such as habitat change or food provisioning .[6-9] To discriminate between these hypotheses we compiled information from 18 chimpanzee communities and 4 bonobo communities studied over five decades. Our data include 152 killings (N=58 observed, 41 inferred, and 53 suspected killings) by chimpanzees in 15 communities and one suspected killing by bonobos. We found that males were the most frequent attackers (92% of participants) and victims (73%); most killings (66%) involved intercommunity attacks; and attackers greatly outnumbered their victims (median 8:1 ratio). Variation in killing rates was unrelated to measures of human impacts. Our results are compatible with previously proposed adaptive explanations for killing by chimpanzees whereas the human impact hypothesis is not supported.

Substantial variation exists in rates of killing across chimpanzee study sites.[2-5,10-12] The human impact and adaptive strategies hypotheses both seek to explain this variation, but have contrasting predictions, which we test here (Tables 1, 2). The human impact hypothesis states that killing is an incidental outcome of aggression, exacerbated by human activities such as deforestation, introducing diseases, hunting or providing food. Accordingly, lethal aggression should be high where human disturbance is high.[8]

In contrast, the adaptive strategies hypothesis views killing as an evolved tactic by which

killers tend to increase their fitness through increased access to territory, food, mates or other benefits.[1-5,10-17] Kin selection[18] and evolutionary game theory[19] yield a set of specific predictions for how benefits and costs should vary with the context, age, sex, and genetic relatedness of the attackers and targets. Lethal aggression occurs within a diverse set of circumstances, but is expected to be most commonly committed by males; directed towards males; directed towards non-kin, particularly members of other groups; and committed when overwhelming numerical superiority reduces the costs of killing. Previous studies have developed and tested these specific hypotheses[2,5,11-17]; the present study represents the first effort to test multiple hypotheses simultaneously with a comprehensive dataset. To do so, we assembled data from communities of eastern (N=12) and western (N=6) chimpanzees[24] studied over 426 years (median = 21 years; range: 4—53) and from 4 bonobo communities studied for 92 years (median = 21; range: 9—39; Figure E1). We rated each case of killing as observed, inferred, or suspected (see Online Methods; Tables E1-E4). To be conservative, we limited our analyses to those rated "observed" and "inferred" unless otherwise noted. We examined contrasting predictions relating to overall patterns of killings (Table 1) and variation among communities (Table 2).

Bonobos are consistently found to be less violent than chimpanzees,[2,23] and lower rates of killing are reported for western than eastern chimpanzees.[2,11] The human impact hypothesis could in theory ascribe these variations to different levels of disturbance. In contrast, in behavioral ecology, distinct populations are expected to respond to prevailing ecological circumstances through biological evolution and/or phenotypic flexibility. For bonobos and western chimpanzees, ecological factors apparently allow relatively high gregariousness, which reduces the risk of experiencing a lethal attack.[2,11] Our dataset covers all major studies of both species of *Pan*, which include sites with and without a history of provisioning, and

with high and low levels of human *disturbance*, a rating estimated independently by each site's director(s) (Online Methods; Figures E1a, E2a).

We documented killings by chimpanzees in 15 of 18 communities (58 observed, 41 inferred, and 53 suspected cases; Tables E1-E4) (Figure 1). For bonobos, we documented only a single (suspected) case, which occurred at Lomako, a never-provisioned site with a low disturbance rating. No killings were recorded at other bonobo sites, including one with a history of provisioning and a high disturbance rating (Wamba). Controlling for years of observation, chimpanzees had a higher rate of killing than bonobos; this difference was statistically significant for eastern but not western chimpanzees (Poisson regression: N=22 communities; estimated coefficients±SE for chimpanzees compared to bonobos: β_0=-4.5±1.0; β_{east}=3.4±1.0, z=3.3, P=0.0008; β_{west}=0.65±1.2, z=0.56, P=0.57; overall effect of clade: χ^2=80.8, df=2, P<0.0001). This difference persisted when "suspected" cases were included (Table E5a.).

To investigate which factors best explained variation in killing rates among chimpanzee communities, we used an information theoretic approach,[25] controlling for years of observation. We considered three variables for the human impact hypothesis: *provisioned* (whether the community had been artificially fed); *area* (size of protected area, with smaller areas assumed to experience more impacts); and *disturbance*. We also considered three variables for the adaptive strategies hypothesis: *clade* (eastern and western chimpanzees may have different histories of selection for violence); *males* (number of adult males, which may influence rates of killing via intensity of reproductive competition and/or coalitional fighting power), and *density* (number of individuals per km^2, which may affect frequency of intercommunity encounter and/or intensity of resource competition). We consider *density* to

reflect natural food abundance. For example, at Ngogo (4.5 chimpanzees/km^2), vegetation sampling revealed high forest productivity[26] and chimpanzees have high C-peptide levels,[27] indicating high energy balance; whereas at Fongoli (0.37 chimpanzees/km^2), chimpanzees range widely across a dry savanna with sparse food.[28] *Density* was unrelated to *disturbance* (general linear model, $F_{1,16}$=1.4, P=0.26).

Of the 16 models we considered (Table 3), four of the five models in the resulting 95% confidence set included combinations of the adaptive variables; the fifth model included the three human impact variables. The best model included only *males* and *density*, and was supported 6.8 times more strongly than the human impact model (evidence ratio = w_i/w_j = 0.40/0.059=6.8). Considering model-averaged parameter estimates,[25] increases in *males* and *density* increased the number of killings; for all other parameter estimates, the 95% CI included zero (Table 3; Figure 2). Excluding one community (Ngogo) that had both an unusually high killing rate and unusually many males resulted in similar values for model-averaged parameters, but only the estimate for *density* excluded zero from the 95% CI (Table E5b; N = 17).

Opposite to predictions from the human impact hypothesis (Table 2), *provisioned* and *disturbance* both had negative effects; the estimates for these parameters included zero in the 95% CI (Table 3; Figure E2b). The highest rate of killing occurred at a relatively undisturbed and never-provisioned site (Ngogo); chimpanzees at the least disturbed site (Goualougo) were suspected of one killing and inferred to have suffered an intercommunity killing; and no killings occurred at the site most intensely modified by humans (Bossou).

As a test of confidence, we investigated the effects of including "suspected" cases and data from bonobos. Including "suspected" cases changed *western* and *provisioned* from negative to positive (Table E5b). Nonetheless, even with these suspected cases, none of the estimates for human impact variables excludes zero from the 95% CI. Including bonobo data widened the confidence intervals for *density* (Table E5b), likely because two bonobo communities had high densities (Figure E1a). With either suspected cases or bonobo data added, only for *males* did the 95% CI exclude zero (Table E5b). Thus, while demographic variables explain variation in rates of killing better than human impact variables, the confidence intervals are sensitive to including suspected cases or data from another species (bonobos).

These analyses combine killings committed for varied reasons by individuals in different age-sex classes. A full explanation of these events requires a finer grained analysis. To this end, we examined variation over time and among different categories of attacker and victim.

Increasing human impacts have been proposed to cause increasing numbers of killings in recent years.[8] However, controlling for changes in the number of communities observed per year (*communities*), the rate of killing has not changed over time (*year*). Using an information theoretic approach[25] to compare three different models (*year*; c*ommunities*; and *year* + *communities*), the best model contained only *communities*; considering model-averaged parameters, the 95% CI excluded zero for *communities,* but not *year* (Poisson regression: N=52 years; model-averaged parameters and 95% CI: β_0=10 (-38—58); β_{year}= -0.0058 (-0.022—0.010); $\beta_{communities}$ = 0.18 (0.10—0.26); Table E5c).

Killings involved a median of five male attackers (range: 0—19) and no females (range: 0—6). Considering all cases for which the number of attackers was observed (N=58) or could be inferred (N=6), males constituted 92% of participants in attacks (338/366). Controlling for observation time and community composition, males were much more likely to participate in killings than females (negative binomial mixed model: N = 36 observations (fixed effects: *sex* with 2 levels; random effects: *community* with 18 levels); β_0=-6.9±0.98; β_{males}=2.6±0.59, z=4.42, P<0.0001). Females sometimes joined males in attacking grown individuals (N=3), but when acting without males, females killed only young infants (N=8).

Controlling for observation time and community composition, males and infants had the highest probability of being killed (Table E6). Notably, during infanticides, attackers sometimes removed infants from mothers under circumstances in which they appeared capable of killing the mother as well, but did not do so.

Most victims were members of different communities from the attackers (N = 62 of 99 cases; 63%) and thus not likely to be close kin.[29] This difference is particularly striking given that chimpanzees could potentially attack members of their own community on a daily basis, but rarely encounter members of other communities (e.g., 1.9% of follow days at Kanyawara[30]).

Intercommunity killings mainly involved parties with many males (median = 9 males, range: 2—28, N=36 cases with known numbers of attackers) attacking isolated or greatly outnumbered males or, more often, mothers with infants (median = 0 males, range: 0—3, N=30; median = 1 female, range: 0—5, N=31). For 30 cases in which the number of adult and adolescent males and females on each side were known, attackers outnumbered

149 defenders by a median factor of 8 (range: 1—32; Table E7). Most intercommunity killings
150 thus occurred when attackers overwhelmingly outnumbered victims.
151
152 Several robust patterns emerge from these data. Killing was most common in eastern
153 chimpanzees and least common among bonobos. Among chimpanzees, killings increased
154 with more males and higher population density, whereas none of the three human impact
155 variables had an obvious effect. Male chimpanzees killed more often than females, and killed
156 mainly male victims; attackers most frequently killed unweaned infants; victims were mainly
157 members of other communities (and thus unlikely to be close kin); and intercommunity
158 killings typically occurred when attackers had an overwhelming numerical advantage. The
159 most important predictors of violence were thus variables related to adaptive strategies:
160 species; age-sex class of attackers and victims; community membership; numerical
161 asymmetries; and demography. We conclude that patterns of lethal aggression *Pan* show little
162 correlation with human impacts, but are instead better explained by the adaptive hypothesis
163 that killing is a means to eliminate rivals when the costs of killing are low.
164
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253 Figure 1: **Number of victims killed per year by members of study communities**. Bars
254 indicate the annual rate of observed (black), inferred (grey), and suspected (white) killings by
255 each community for bonobos (B; N=4), eastern chimpanzees (E; N=12), and western
256 chimpanzees (W; N=6). Communities with a history of provisioning are indicated by (P).
257
258 Figure 2: **Number of killings per year for each community versus a, number of males**
259 **and b, population density (individuals/km^2).** Rates for each community are indicated by
260 black diamonds (chimpanzees; N=18) and open squares (bonobos; N=4). Black lines indicate
261 simple linear regression for chimpanzee data for illustrative purposes only; statistical tests
262 were done using Poisson regressions.

263 **Table 1. Predicted patterns of lethal aggression**

No.	Variable	Human Impact Hypothesis	Adaptive Strategies Hypothesis
1.	Chimpanzees kill more than bonobos	None	+
2.	Rate of killing over time	+	None
3.	Sex bias: attackers	None	Mainly males
4.	Sex bias: victims	None	Mainly males
5.	Age of victims	None	Mainly young infants (most vulnerable and/or reduce time to mother's next estrus)
6.	Genetic relatedness of attackers and victims	None	Mainly non-relatives (e.g., members of other communities)
7.	Numerical asymmetries	None	Victims greatly outnumbered

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265

266 **Table 2. Predicted correlates of number of killings per study community**

No.	Variable	Human Impact Hypothesis	Adaptive Strategies Hypothesis
1.	Provisioning (*provisoned*)	+	None
2.	Size of protected area, km^2 (*area*)	-	None
3.	Disturbance rating (*disturbance*)	+	None
4.	Eastern vs. western chimpanzees (*clade)*	None	+
5.	Mean number of adult males (*males*)	None	+
6.	Mean population density (*density*)	None	+

267

Table 3. Summary of model selection: number of killings per community.

#	*b*	*clade*	*males*	*density*	*area*	*prov.*	*dist.*	*K*	Δ_i	w_i
1	-3.6		0.081	0.21				4	0.00	0.40
2	-2.3	-1.9	0.073					4	0.61	0.30
3	-3.1	-1.4	0.073	0.15				5	1.8	0.16
4	-2.7		0.087					3	3.4	0.07
5	7.1				-0.0016	-1.4	-0.63	5	3.8	0.06
6	-2.2	2.4	0.10	0.42	-0.00083	1.3	-0.27	8	10	0.00
7	3.7				-0.0011		-0.40	4	12	0.00
8	-2.0	-2.1		0.17				4	17	0.00
9	-1.2	-2.7						3	18	0.00
10	-2.8			0.28				3	21	0.00
11	-1.1				-0.00042			3	24	0.00
12	-1.1				-0.00042	-0.12		4	28	0.00
13	-1.5							2	34	0.00
14	-1.6					0.19		3	36	0.00
15	-1.4						-0.011	3	37	0.00
16	-1.6					0.18	-0.0046	4	40	0.00
MAP	-2.4	-0.78	0.073	0.11	-0.00010	-0.078	-0.038			
2.5%	-5.0	-1.8	0.053	0.00029	-0.00027	-0.24	-0.11			
97.5%	0.12	0.25	0.093	0.22	0.000083	0.082	0.033			

Parameters include the intercept (*b*); impact of western relative to the eastern *clade* of chimpanzees; mean number of adult males per community (*males*); mean population density per community (*density*); size of protected area in km^2 (*area*); history of regular provisioning with food (*prov.*); disturbance rating (*dist.*); the number of free parameters (*k*) including the dispersion parameter (ĉ); the difference in Akaike information criterion (corrected for overdispersion: QAICc) between the *i*th model and the best model (Δ_i); and model weight (w_i). Models are arranged in order from best (lowest $\Delta QAICc_i$) to worst (highest ΔQAICc). The weight of the model (w_i) is the probability that a given model is the best model in a given set of models. Model-averaged parameter estimates (*MAP*) with upper (97.5%) and lower (2.5%) bounds of the 95% confidence intervals are given in the bottom rows.

281 **Methods**

282

283 **Rating of cases.** We rated a case as *observed* if observers directly witnessed the attack. We
284 rated a case as *inferred* if the attack was not directly witnessed, but compelling evidence
285 indicated that the victim was killed by chimpanzees (such as a body found with multiple bite
286 wounds, and/or skeletal trauma consistent with a chimpanzee attack). We rated other cases as
287 *suspected*; for example, disappearances of chimpanzees that appeared healthy prior to their
288 disappearance (with the exception of adolescent females, who generally disperse from their
289 natal community), or individuals known to have died from wounds that may have been
290 inflicted by chimpanzees.

291

292 **Demographic data.** For each community, we used the number of individuals known to be
293 alive in each age-sex category on 01 January of each year to obtain the mean number of
294 individuals in each category and summed to obtain the mean total group size. We calculated
295 the mean number of males and females in four age categories: ≥ 12 (old enough to participate
296 in intergroup fighting and reproductive competition); ≥8, <12 (older juveniles to young
297 adolescents); ≥3, <8 (older infants to young juveniles); and <3 years (young, vulnerable,
298 unweaned infants). For each community, the number of individuals known to be alive in each
299 age-sex category on 01 January of each year was averaged to obtain the mean number of
300 individuals in each category and summed to obtain the mean total group size.

301

302 **Human disturbance scores.** We scored human disturbance as the sum of five separate
303 ratings adapted from[31], each scored on a 1 to 4 point scale, giving a possible range of 5–20
304 points: (1) disturbance to habitat; (2) degree of harassment of study animals by people; (3)
305 amount of hunting of study animals; (4) degree of habituation to human observers at

beginning of studies; and (5) whether major predators have been eliminated (on the assumption that the elimination of major predators by humans is associated with higher levels of human impact). The different measures of disturbance were not strongly inter-correlated. Of the 10 pairwise comparisons among the 5 measures, the median correlation coefficient for the 22 study communities was 0.24 (range: -0.06—0.78). The two pairs that had a correlation coefficient higher than 0.5 were (home range)(harassment)=0.78, and (harassment)(predators)=0.52. Thus, communities with high disturbance to their home range habitat also suffered more harassment by people, and communities with more harassment by people also had fewer natural predators remaining in their habitat. The median variance among the 5 measures was 1.0 (range: 0.7—1.4). None of these variances differed significantly from the others (F-tests: $P>0.05$).

Statistical tests. We conducted statistical tests using *R* 3.0.2.[32] To test for differences in rate of killing between bonobos and the two clades of chimpanzees (eastern and western[24]), we conducted Poisson regressions with log(*years of study*) as an offset. The fact that bonobos had the same response for all communities (zero observed/inferred killings) resulted in a complete separation problem.[33] We addressed this by doing a series of four Poisson regressions, each time replacing the 0 killings for one of the four bonobo communities with 1 killing to make the data less extreme, and averaging the results. This provides a conservative estimate of the difference in rates of killing between chimpanzees and bonobos.

To investigate which factors best explained the number of killings per chimpanzee community, we examined a set of *a priori* specified models, based on hypothesized effects of six independent variables: *clade*; *males* (mean number of males ≥12 years old), *density* (mean number of individuals per community/home range (km^2); *area* (size (km^2) of national park or

331 reserve in which community resided); *provisioned* (whether the community had a history of
332 being regularly provisioned with food by researchers) and *disturbance* (sum of five four-
333 point ratings, based on[31]). Each model consisted of a Poisson regression with the total count
334 of observed/inferred killings committed by each community as the dependent variable, and
335 log(*years of study*) as an offset. We recognize that *years of study* is a rather coarse-grained
336 measure of observation time, but finer grained measures such as total number of observation
337 hours were not available for all communities. We selected models to distinguish between the
338 predictor variables most closely associated with the adaptive strategies hypothesis (*clade*,
339 *males*, and *density*) and the human impact hypothesis (*protected area*, *provisioned* and
340 *disturbance*), including the null model, models with each variable by itself, combinations of
341 up to three variables associated with each hypothesis, and the full model. We limited the
342 number of variables per model to avoid over-fitting, and limited the number of models tested
343 to reduce the risk of finding spurious correlations. We corrected for overdispersion and small
344 sample size using QAICc, ranked models according to QAICc score (lowest=best), and used
345 results from all models to calculate model-averaged estimates of parameters.[23]
346
347 To test for sex differences in participation in lethal aggression, we conducted a GLMM with
348 negative binomial error structure using the glmmADMB package.[34] For the dependent
349 variable, we used the number of *participations* in killings by each sex for each community.
350 We defined *participation* as the active involvement of an individual during a lethal attack
351 (e.g., making or attempting to make direct aggressive contact with the victim). For each case
352 for which the attackers were observed directly, or could be inferred with confidence, we
353 counted the number of attackers of each sex. For each community, we summed the number of
354 attackers across all cases to obtain the number of times individuals of each sex participated in
355 attacks. Independent variables consisted the fixed effect *sex* (2 levels: *male* and *female*) and

356 the random effect *community* (18 levels). To control for community composition, we used
357 log(*chimp-years*) for each sex in each community as an offset. *Chimp-years* was defined for
358 each age-sex class as *years of study* multiplied by the mean number of individuals of that
359 age-sex class present in the victim's community.
360
361 To test for patterns in the age-sex class of victims, we conducted a GLMM with Poisson error
362 structure using the lme4 (1.0-5) package.[35] To control for possible sex differences in
363 motivation for killing, we excluded from analysis the 8 cases that were known to have been
364 committed solely by females. For the dependent variable, we used the number of observed
365 and inferred victims of each age-sex class for each community. Independent variables with
366 fixed effects were *sex* (2 levels) and *age-class* (four levels, as categorized above
367 (Demographic Data)) and the random effect *community* (26 levels: 18 habituated
368 communities and 8 unhabituated communities (victims of intercommunity killings by study
369 communities). Because one community (Kahama) had zero adolescent males, and the number
370 of infants and juveniles were not specified for another (Kalinzu), the total number of age-sex
371 class and community combinations in our analysis (N=203) was less than would be if all age-
372 sex classes were represented for each community ((2 sexes)x(4 age classes)x(26
373 communities)=208). To control for the composition of the different communities, we used
374 log(*chimp-years*) as an offset. For unhabituated communities, for which demographic
375 information was not available, we defined *chimp-years* as the number of years of observation
376 of the focal community (the community being observed when the killing occurred),
377 multiplied by the median number of individuals of that age-sex class present in the median
378 chimpanzee community. Because the range size and membership of unhabituated
379 communities was not known, we assigned victims to no more than one unhabituated
380 community per study community; this undoubtedly underestimates the total number of

communities involved, but should not affect the goal of this analysis, which was to estimate the effect of age and sex class on the risk of being killed, given the proportion of each age-sex class in the population. For chimp-years for victims of unknown sex, we used the mean number of males and females present for that age class. To keep type I error rate at the nominal level of 5% we included random slopes of each level of the fixed effects *sex* and *age-class* within the random effect *community*.[36,37]

Additional citations for Online Methods

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405 **Extended Data**

406

407 **Figure E1. Summary data and location of study sites**. **a,** Summary data for each
408 community. *Clade*: bonobos (B), eastern chimpanzees (E), western chimpanzees (W);
409 *Community*: mean total size of the community; *Males*: mean number of males ≥12 years old;
410 *Females*: mean number of females ≥12 years old; *Home range*: mean size of the
411 community's home range ($km^{2)}$; *Density*=(*community)*/(*home range)*; *Area*: size of protected
412 area inhabited by the community; *Provisioned*: whether community was regularly
413 provisioned with food; *Disturbance:* sum of the disturbance rating scores. **b,** Location of
414 chimpanzee (circles; N=10) and bonobo (squares; N=3) study sites in Africa.

415

416 **Figure E2**. **Disturbance ratings**. **a,** Disturbance ratings for each site: disturbance to habitat
417 (black bars); harassment of study animals by people (vertical lines); amount of hunting of
418 study animals (grey); degree of habituation to people at start of study (diagonal hatching);
419 and whether major predators have been eliminated (white). *Clade* is indicated by letters
420 following community name: bonobos (B), eastern chimpanzees (E), and western
421 chimpanzees (W). **b,** Number of killings per year vs. disturbance. Rates for each community
422 are indicated by black diamonds (chimpanzees; N=18) and open squares (bonobos; N=4).

423

424 **Table E1: Intercommunity killings of weaned victims**. For Tables E1-E4, *Ref.*
425 (*References*) refers to references in Table E8.

426

427 **Table E2: Intercommunity infanticides**

428

429 **Table E3: Intracommunity killings of weaned victims**

Table E4: Intracommunity infanticides

Table E5: Summary of model averaged parameters using different subsets of the data. **a,** Species-level comparison of rates of killing between bonobos and chimpanzees. Using only observed and inferred cases (Row 1) results in a complete separation problem (and thus undefined 95% CIs); which is resolved when including either the one suspected case for bonobos (Row 2) or all suspected cases for both species (Row 3). **b,** Community-level comparisons of factors affecting rates of killing focusing either within chimpanzees (Rows 1-3) or including bonobos (Row 4). For comparison, the model-averaged parameter estimates from Table 3 (observed and inferred cases only) are presented in Row 1. Rows 2-4 show the effects of including suspected cases, excluding the unusually large Ngogo community, and adding bonobos, respectively. For the analysis presented in Row 4, the suspected case for bonobos has been included to prevent a complete separation problem. **c,** Summary statistics showing that, controlling for the number of communities under observation, the number of killings observed per year has not increased.

Table E6. Summary of parameter estimates for test of the effect of age and sex on probability of being killed. Poisson regression; N=203 combinations of *sex*, *age class* and *community*; fixed effects: *sex* with two levels (*male, female*); *age class* with four levels (*infant, juvenile, adolescent, adult*); random effects: 26 levels of *community*, including 8 unhabituated communities; log-likelihood = -123. The effect of different age classes is in comparison with *adolescent*; the effect of male is in comparison with *female*. We confirmed the statistical significance of the fixed effects by comparing the full model with the null model (with just

454 the random effects: χ^2= 32.7, df=4, P<0.0001) and a reduced model with sex, but not age-

455 class, as a fixed effect (χ^2= 14.4, df=3, P=0.002).

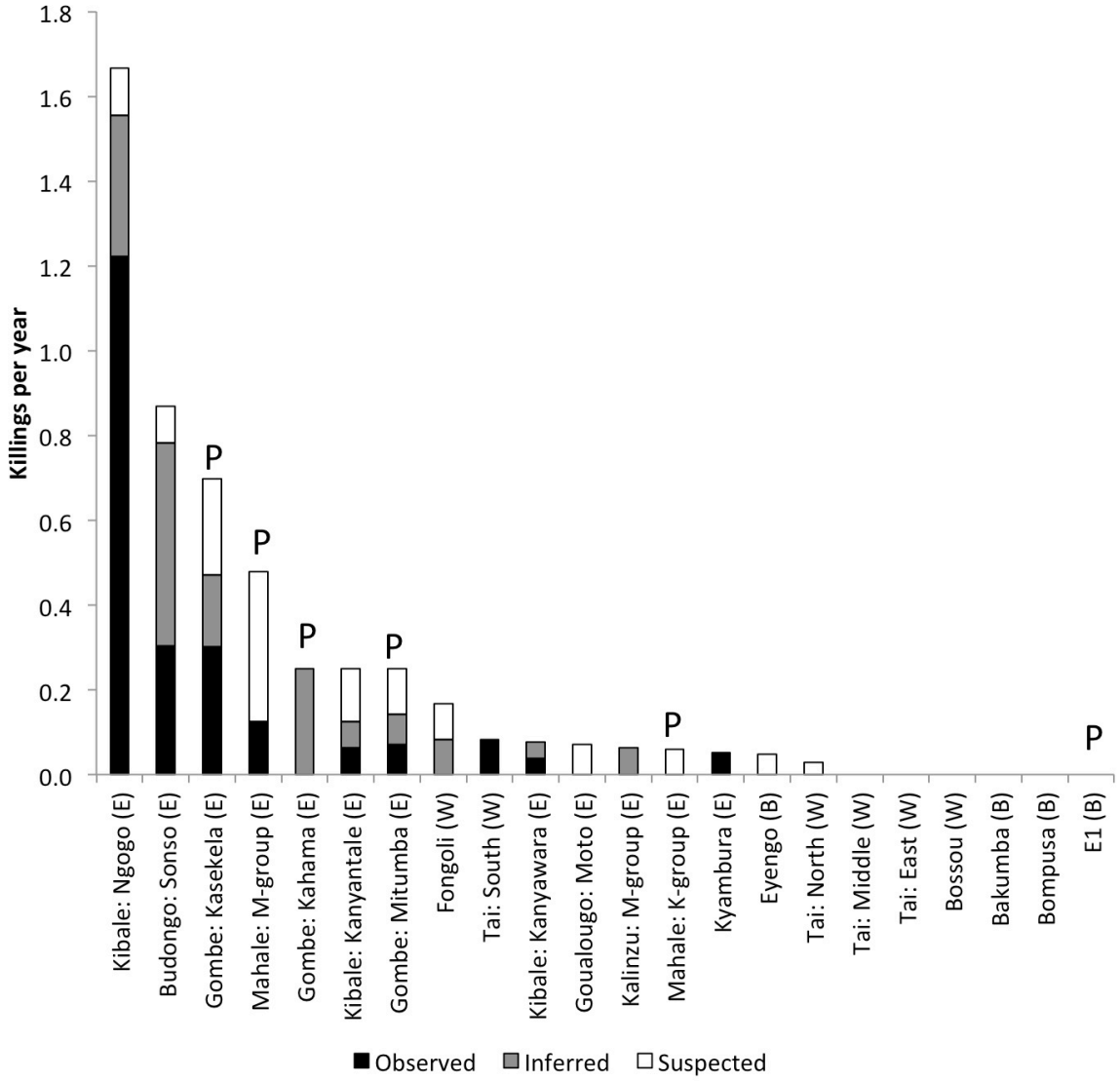
456

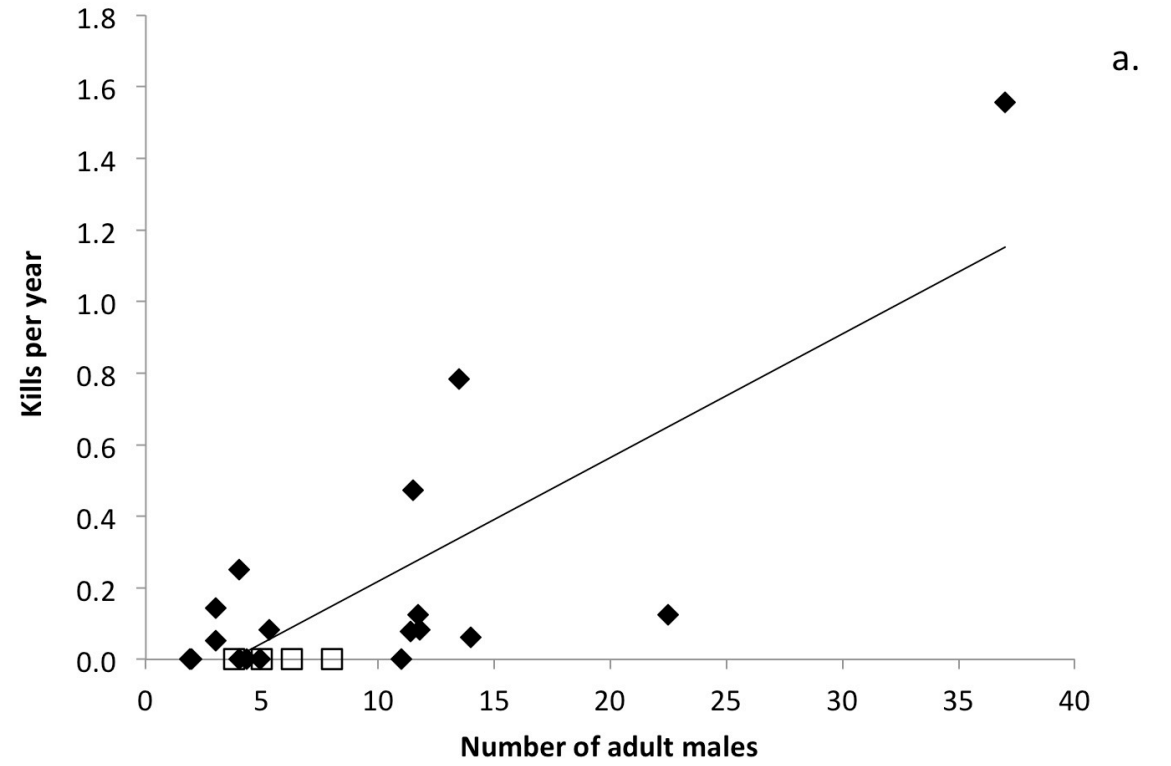
457 **Table E7: Number of attackers and defenders on each side for intercommunity killings.**

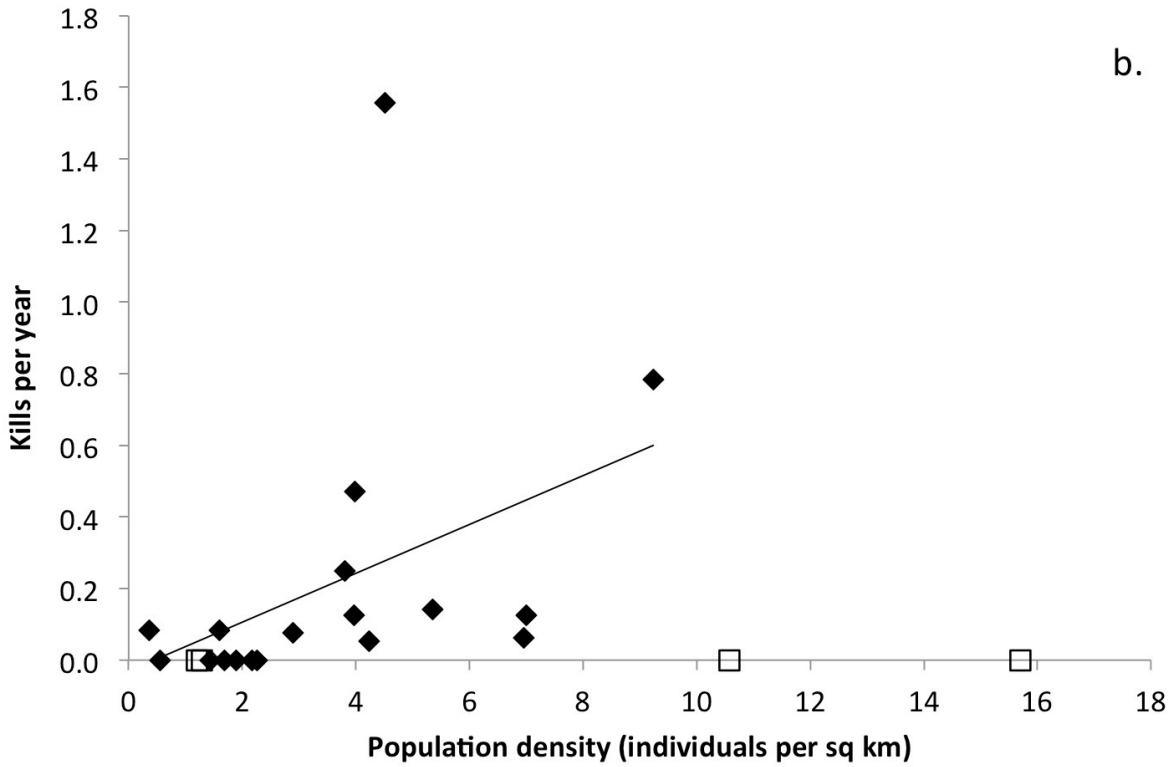
458

459 **Table E8: References for data in tables E1-E4.**

460


Killings per year
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
P
P
P
P
P
P
Kibale: Ngogo (E)
Budongo: Sonso (E)
Gombe: Kasekela (E)
Mahale: M-group (E)
Gombe: Kahama (E)
Kibale: Kanyantale (E)
Gombe: Mitumba (E)
Fongoli (W)
Tai: South (W)
Kibale: Kanyawara (E)
Goualougo: Moto (E)
Kalinzu: M-group (E)
Mahale: K-group (E)
Kyambura (E)
Eyengo (B)
Tai: North (W)
Tai: Middle (W)
Tai: East (W)
Bossou (W)
Bakumba (B)
Bompusa (B)
E1 (B)
Observed
Inferred
Suspected


a.
Kills per year
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
35
40
Number of adult males


b.
Kills per year
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
14
16
18
Population density (individuals per sq km)